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Studies of some new cases of apogamy in ferns

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(WITH PLATES 4 AND 5)

Introduction

During the past six years, the writer has made an attempt to determine towhat extent undernormal cultural conditions apogamy occurs in the homosporous leptosporangiate ferns and especially in the genera *Pellaea*, *Pteris*, and *Aspidium*. Since the nuclear history in only a few apogamous ferns has been investigated, it was believed that further studies in the cytology of such ferns would be desirable. Hence an investigation of this nature was undertaken in the species in which apogamy was discovered, and this part of the work has been considered more interesting and important than the discovery of new cases of apogamy. In some of the ferns studied the nuclear history is wholly or partly known, but the discussion of this subject is reserved for another paper. At this time new cases of apogamy will be reported and briefly considered.

Methods and materials

On account of the great difficulty experienced in securing spores for cultural work, the investigation, so far as the discovery of new cases of apogamy is concerned, cannot be regarded as wholly successful. Some of the spores were collected in the field. A large number of plants were grown in the university greenhouse, and

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spores were collected from these. Spores from a still larger number of species were obtained through the kindness of the following persons: Dr. A. B. Stout, New York Botanical Garden; Dr. R. C. Benedict, Brooklyn Botanic Garden; Dr. G. T. Moore, Missouri Botanical Garden; Dr. E. B. Copeland, Los Banos, Philippine Islands; Mr. F. C. Greene, Rollo, Missouri; and Rev. George Moxley, Los Angeles, California. To these gentlemen the writer wishes to express his sincerest thanks, for in no small measure they contributed to the investigation.

The spores were generally sown on the surface of a nutrient solution or on sphagnum. The latter was placed in a Stender dish and saturated with a nutrient solution. Before sowing the spores, the medium was thoroughly sterilized. Other media, such as nutrient agar, peat clay and loam, were also used, but none of these proved as satisfactory for the cultural work as the sphagnum. The Stender dishes were placed under bell-jars in a Wardian case in the university greenhouse. The jars were tilted on edge, so that the prothallia were provided with a sufficient supply of oxygen and carbon dioxid. The temperature of the Wardian case varied from 65° F. in winter to about 110° F. in summer. The prothallia were protected from too intense illumination by shading. The light was very favorable for the growth of fern prothallia since, when they were not crowded in the cultures, they became heart-shaped. The moisture supply was always sufficient for fertilization to occur in the non-apogamous species grown at the same time under precisely the same cultural conditions.

In a large number of species in which fertilization is known to occur, including *Pteris aquilina* L., *P. serrulata* L., *Osmunda regalis* L., *O. Claytoniana* L., *O. cinnamomea* L., and *Adiantum pedatum* L., sex organs were produced under the conditions just described, and embryos were formed only as a result of the union of the gametes.

The prothallia of *Nephrodium molle* Desv. and *Asplenium nidus* L., in which Yamanouchi (1908) and Nagai (1914) respectively induced apogamy, were grown under the same conditions, but while embryos were produced in large numbers, none were formed apogamously.

The spores of some of the apogamous species were sown on soil

in the university greenhouse, but the prothallia never showed any peculiarities in their development, and embryos were never produced by fertilization. Hence it appears that cultural conditions were not a factor in inducing apogamy in any case.

In the majority of cases, the prothallia were grown until embryos were formed, either as a result of fertilization or apogamously. Parthenogenesis was not excluded in the non-apogamous species. To determine this point a cytological investigation would have been necessary.

The conclusions are in no case based on a single culture but on a large number of cultures. Cultures in which only a few prothallia were obtained were always discarded. Great care was exercised in handling the spores before sowing in order to avoid, so far as possible, mixing those of different species.

Two sets of cultures were made of each of the ferns tested for apogamy. In one set only a small number of spores were sown to avoid crowding the prothallia. The prothallia under these conditions grew to a good size and became heart-shaped. It was believed that these cultures were favorable for the development of archegonia. The other cultures were made by sowing a large number of spores. The majority of the prothallia in these cultures were irregular in form and usually produced numerous antheridia. If embryos were produced, they appeared in both types of cultures. From the two sets of cultures it was possible to determine whether sex organs developed.

While the prothallia of the different species were growing, they were carefully examined from time to time with a microscope. Since in a number of species investigated tracheids appeared among the prothallial cells, it was not difficult to determine the apogamous forms. In all the apogamous species a region composed of small cells made its appearance posterior to the apical notch. In every instance when such an area of small cells appeared on the surface of the prothallium, the embryo proved to be of apogamous origin. When archegonia were produced in any of the apogamous species, they were absent on many of the prothallia. These, however, always produced embryos apogamously. In some species longitudinal sections of the prothallia were made in order to determine with more certainty the origin of the embryo.

APOGAMY IN PELLAEA AND NOTHOLAENA

The first case of apogamy in the genus *Pellaea* was discovered by Goebel (1905) in *P. nivea* (Poir.) Prantl. Later Woronin (1907, 1908) found apogamy in *P. flavens* (Sw.) C. Chr., and *P. tenera* (Gill.) Prantl., and also in *Notholaena Eckloniana* Kunze and *N. sinuata* (Lag.) Kaulf., belonging to a genus closely related to *Pellaea*. Berggren (1888), however, had already described apogamy in *N. distans* R. Br. The writer has described apogamy in *Pellaea atropurpurea* (L.) Link (Steil, 1910) and *P. adiantoides* J. Sm. (Steil, 1915*b*). New cases have since been found in *P. atropurpurea* var. *cristata* Trelease and *P. viridis* (Forksk.) Prantl.

APOGAMY IN PTERIS

Farlow (1874) discovered apogamy in *P. cretica* L. var. *albolineata* Hort. This was the first reported case in plants. Up to the present time, no other case of apogamy has been reported in any other species of *Pteris*, although Stephens and Sykes (1910) assumed that apogamy occurred in *Pteris Droogmantiana* L. Linden, on account of the presence of binucleate cells in the prothallia.

Wigand (1849) appeared to be convinced that the fern embryo did not owe its origin to fertilization. He undoubtedly described apogamous embryos, and from his descriptions and figures it is probable that he studied the development of such embryos in some species of *Pteris*. Although Wigand gives a good description of an apogamous embryo, the true nature of apogamy was first recognized by Farlow.

Tracheids were observed in the prothallium of *P. sulcata* Meyen by Leszczyc Suminski (1848). Later Mercklin (1850) confirmed the observation. Neither, however, knew the significance of the presence of such sporophytic tissue elements in the cells of the gametophyte. DeBary (1878) grew the prothallia of *P. quadriaurita* Retz. var. *argyraea* Moore but failed to find the fern apogamous.

Several years ago, without a knowledge of the observations of these investigators, the writer discovered apogamy in *P. sulcata*. Spores were obtained from the New York Botanical Garden, and

from Dr. E. B. Copeland, Los Banos, Philippine Islands. A plant obtained from Mr. Anderson, fern specialist, Short Hills, New Jersey, was grown in the university greenhouse, and spores were also collected from this plant. Archegonia were never found on any of the prothallia. However, apogamous embryos in large numbers were produced. Since numerous cultures of *P. sulcata* were made and from spores obtained from different plants, there can be no doubt that apogamy is of constant occurrence in the fern.

P. argyraea Moore has also been found by the writer to be apogamous. In many respects the prothallia and apogamous embryos are similar to those of *P. sulcata*.* In *P. Parkeri* Hort. The writer has also discovered apogamy. The prothallia become large as compared with those of the former but develop in a similar manner.

During the course of the investigation a large number of *P. cretica* varieties have been tested for apogamy, and so far none have been found which form embryos as a result of fertilization. The following is a list of these apogamous horticultural varieties: *albo-lineata Alexander*, *maxima*, *magnifica*, *Mayii*, *major*, *Wimsettii*, *Wimsettii compacta*, *Wimsettii multiceps*, *Wimsettii grandis*, and *Ouvrardi*. For the identification of some of the above varieties the writer is indebted to Mr. James C. Clark, of Philadelphia. *P. cretica* var. *albo-lineata Alexander* Hort. resembles the *P. cretica albo-lineata* in which Farlow discovered apogamy only in its second set of leaves, which are linear but with a broader band of white along the main veins of the pinnae. The first leaves are nearly all crested, while the linear leaves show sometimes a slight tendency to become crested. From the investigations which have already been made, it may be predicted that all *Pteris cretica* forms are apogamous. Apogamy has not so far been found in any of the varieties of *P. serrulata* L. f.

APOGAMY IN ASPIDIUM

Apogamy was found by De Bary (1878) in *Aspidium falcatum* (L. f.) Sw. and in a crested cultivated variety of *A. Filix-mas* (L.)

* According to Christensen (Ind. Fil. 593, 608. 1906) *P. sulcata*, *P. quadriaurita* and *P. argyraea* are all synonyms of *P. biaurita* L. According to Underwood and Benedict (Bailey's Stand. Cycl. Hort. 2852. 1916) *P. quadriaurita* is distinct from *P. biaurita*, *P. argyraea* being given as a var. *argyraea* Hort. under *P. quadriaurita*.

Sw. ("*A. Filix-mas cristatum*"). In the former Miss Allen (1911) described nuclear and cell fusions in the sporangia, previous to the formation of the spores. Kny (1895) discovered apogamy in an uncrested form of *A. Filix-mas* ("*A. Filix-mas genuinum*"). Lang (1898) found apogamy in the aberrant varieties of *A. Filix-mas*, known as "*Nephrodium pseudo-mas* var. *polydactylum* Wills" and *N. pseudo-mas* var. *polydactylum* Dadds." In these same varieties (discussed under the name "*Lastrea pseudo-mas* var. *polydactyla*"), Farmer, Moore and Digby (1903) and Farmer and Digby (1907) described remarkable nuclear fusions in the prothallium before the formation of the apogamous embryos. In a preliminary note on apospory Miss Digby (1905) had already reported apogamy in "*Lastrea pseudo-mas* var. *cristata apospora* Druery."

Heilbron (1901) found apogamy in *Aspidium aculeatum* (L.) Sw. var. *cruciato-polydactylum* Jones and *A. angulare* Willd. forma *grandidens* Moore. Five years later (Steil, 1915 *a* and *b*) apogamy was reported in *A. hirtipes* Bl. (*Nephrodium hirtipes* Hook.), *A. Tsus-Simense* Hook. and *A. chrysolobum* Kaulf. (*Lastrea chrysoloba* Presl). Apogamy has also been discovered as a result of the investigations herein described in *A. varium* (L.) Sw., *A. auriculatum* (L.) Sw., *A. caryotideum* Wallich, *Cyrtomium Fortunei* J. Sm. and *C. Rochfordianum* Hort.*

THE DEVELOPMENT OF THE PROTHALLIA AND SEX ORGANS

In all the species so far studied, the prothallia become typically heart-shaped. Between the prothallia of apogamous and non-apogamous species no difference was noted excepting that in the latter tracheids sometimes appear. The prothallia of all the species of *Aspidium* in which apogamy has been discovered bear glandular hairs on both surfaces and on the margins (PLATE 4, FIGS. 1, 2, and 5; PLATE 5, FIGS. 20 and 21), while in both *Pellaea* (PLATE 5, FIGS. 13, 14, and 15) and *Pteris* (PLATE 4, FIGS. 3, 4, and 6) such hairs are always absent. The prothallia in *Aspidium* grow to a much larger size than in *Pellaea* and in most species

* Benedict (Bailey's Stand. Cycl. Hort. 2852. 1916) gives *C. Rochfordianum* as a synonym of *C. falcatum* J. Sm. (= *A. falcatum* Sw.); Christensen (Ind. Fil. 460. 1916) includes both *A. caryotideum* and *Cyrtomium Fortunei* among the synonyms of the same species.

of *Pteris*. Those of *Aspidium chrysolobum*, *A. varium*, and *A. auriculatum* become especially large.

Antheridia are produced on the prothallia of all of the apogamous species. The antherozoids responded to the chemotactic influence of the archegonia of non-apogamous species in all cases in which tests were made. The mature antherozoid appears perfectly normal and is probably capable of functioning. In a former note (Steil, 1910) it was reported that antheridia had not been observed on the prothallia of *Pellaea atropurpurea*, but in many of my cultures made since this time they have been formed in large numbers.

Archegonia have been found on the prothallia of *Aspidium chrysolobum*, but in a large number of the prothallia they are never produced (PLATE 4, FIG. 5). The embryo always appears at the anterior portion of the cushion and can be readily observed to begin its development as a vegetative outgrowth from the prothallial cells. Over 50 per cent. of the prothallia of *Pellaea viridis* bear archegonia. Whether embryos are produced as a result of fertilization in either case has not been determined. In a few instances two embryos were observed to develop from a single prothallium of *P. viridis*. One of these was apogamously produced, but the other appeared to owe its origin to an egg. Archegonia were never found in the prothallia of *P. adiantoides*, and for this reason especial care was exercised in making the cultures of *P. viridis*. Spores were obtained from the New York and the Missouri Botanical Gardens and from two plants grown in the university greenhouse, but the embryos in all of the cultures made from the spores thus obtained were produced apogamously. In some of the *Pteris cretica* varieties archegonia were observed very rarely, but an embryo was never found to be developed from an egg.

THE DEVELOPMENT OF THE APOGAMOUS EMBRYO

The apogamous embryo usually appears as a compact region of small cells on the ventral side of the prothallium and posterior to the apical notch (PLATE 4, FIGS. 2–5, and PLATE 5, FIGS. 13 and 20). When the embryo begins its development, the prothallium has not yet attained its maximum growth. In some species, such as *Aspidium chrysolobum* (PLATE 4, FIGS. 1 and 2), *A. hir-*

tipes and *A. auriculatum*, the prothallia increase considerably in size as the young embryo is developing. In most instances the cushion has not been formed when the embryo makes its appearance. The embryo proceeds in development with the growth of the cushion. On account of the early appearance of the embryo. it was easy to determine when apogamy occurred in any species,

While the embryo usually occurs back of the apical region its position varies in the different species and even in the same species. In some cases the embryo is developed directly in the apical notch (PLATE 5, FIGS. 14 and 15). A cylindrical or conical process produced as an outgrowth of the apical region may bear on some portion of it the apogamous embryo. Sometimes the embryo may be produced at a considerable distance posterior to the notch (PLATE 5, FIGS. 13 and 20). In still other instances the embryo is formed on the lobes of the prothallium (PLATE 5, FIG. 19). From the foregoing, it is seen that the apogamous embryo can be produced on portions of the prothallia where archegonia have never been observed to be formed in any non-apogamous species.

Tracheids are visible among the prothallial cells of some of the apogamous species long before the prothallium has reached its maximum growth (PLATE 4, FIG. 3, and PLATE 5, FIG. 20).

It is usually in the portion of the prothallium where the tracheids appear that the apogamous embryo begins its development. The tracheids are readily observed in many cases, since the prothallium frequently becomes pale in the region of the notch and where these elements are produced. The cells in this portion of the prothallium contain fewer chloroplasts than the neighboring prothallial cells (PLATE 5, FIG. 20). In the species of *Pteris* the tracheids are most frequently observed (PLATE 4, FIGS. 3, 4, and 6). In many instances the light area extends forward as a cylindrical or conical process, already mentioned (PLATE 4, FIG. 6).

The embryo is usually surrounded by hairs, each composed of a single row of cells (PLATE 5, FIG. 13). In some species, as in *Aspidium chrysolobum* and *A. Tsus-Simense*, scales are also produced.

In only a few species has the development of the apogamous embryo been studied in sections. It seems that the apical cell of

the leaf always appears first, then that of the root, and finally that of the stem. A foot has never been observed to develop in any of the species in which the embryos were studied from prepared slides. Usually the leaf is much in advance of the root (PLATE 4, FIG. 9). A leaf, however, may be just making its appearance after the root has grown considerably in length (PLATE 4, FIG. 8). Both root and leaf, in the large majority of cases, are produced on the ventral side of the prothallium (PLATE 4, FIG. 7). PLATE 4, FIG. 12, represents a prothallium with an apogamous embryo the leaves and roots of which are ventral. Either root or leaf or both may appear on the dorsal surface (PLATE 4, FIGS. 10 and 11, and PLATE 5, FIG. 16). In the cultures of *Aspidium chrysolobum* and *A. hirtipes* embryos of this nature have been observed. Such anomalies may be produced by light conditions as Leitgeb (1885) has shown.

As a result of studies thus far made, it has not been determined whether the apogamous embryo owes its origin to a single superficial cell or to inner and outer cells of the prothallium.

Frequently, in some of the cultures, more than one embryo was observed to develop from a single prothallium. This was especially the case when the prothallia showed a tendency to become lobed (PLATE 4, FIGS. 3 and 4). PLATE 4, FIG. 3, represents a prothallium of *Pteris cretica albo-lineata Alexander* with a young embryo posterior to the apical region, and tracheids in each of the two secondary regions of growth. Another prothallium of the same variety is shown in PLATE 4, FIG. 4. In this instance tracheids are present in the apical region, and two embryos have been produced on other portions of the prothallium. One of these is produced in the apical region of one of the main lobes, and the other is a vegetative growth on the inner margin of a lobe itself. Each of these embryos has produced a small leaf, *l*, and a root, *r*. The embryos in such cases, as is readily seen, are wholly independent of one another. In some instances it was observed that some of the tracheids extended from the apical notch of the prothallium to one or both of the inner margins of the lobes where the embryo was produced (PLATE 5, FIG. 19). It may be stated in this connection that embryos are not always produced when tracheids are formed, but in most cases these tissue-elements indicate the beginning of an apogamous embryo.

In one of the cultures of *Pteris sulcata*, conical and nearly spherical projections were observed in the lobes of the prothallia. Some of these prothallia were transferred to another culture, and the growth of the projections was followed in both cultures. The projections produced either secondary prothallia or apogamous embryos. The former were often cylindrical at the point of origin, but in other respects they resembled the ordinary prothallia of *Pteris sulcata*. As many as six embryos were observed on the lobes of a single prothallium. In most instances these were normal, producing both roots and leaves.

By cultural conditions secondary prothallia have been produced from the primary prothallia of many of the apogamous species. These prothallia also form embryos apogamously. DeBary (1878) reported that such prothallia of *Pteris cretica albo-lineata* seldom produced embryos. However, in my cultures of the same species, the secondary prothallia usually produced embryos of apogamous origin. Secondary prothallia of *Pellaea atropurpurea*, *Aspidium hirtipes*, *Pteris sulcata*, *Pteris argyraea*, and *Pteris cretica albo-lineata Alexander* frequently produce apogamous embryos.

THE INFLUENCE OF WEAK ILLUMINATION ON THE DEVELOPMENT OF THE PROTHALLIA AND OF THE APOGAMOUS EMBRYOS

When the prothallia of the apogamous species were placed under the influence of weak light, the same results were obtained as with the non-apogamous ferns. Filaments were formed from the margin and both surfaces of the prothallia (PLATE 5, FIG. 21), and these under the normal conditions of illumination in the wardian case became independent prothallia, which in nearly all instances formed also apogamous embryos. When the prothallia were maintained in weak light, they remained simple or branched filaments, producing neither sex-organs nor embryos (PLATE 5, FIG. 18). Under somewhat more favorable conditions of illumination, ribbon-like plates were produced, which frequently bore numerous antheridia and occasionally apogamous embryos. When the illumination was slightly less than that in the greenhouse, the prothallia became lobed (PLATE 5, FIGS. 14 and 15). In the new apical regions which were formed embryos also made their appearance (PLATE 5, FIG. 17).

The conical or cylindrical processes already described grew considerably in length when the cultures were placed in weak light. In such instances an apical cell could be readily distinguished. The embryo in these cultures was frequently formed on the process, and usually it was produced as a direct outgrowth of the apical notch. The "light" area, or pale portion of the prothallium where the embryo begins its development, remains more conspicuous under these conditions. The colorless plastids, present in large numbers in the cells of the pale region, become chloroplasts under favorable conditions of light, and hence the nearly colorless region is not so clearly differentiated in the latter case.

ATTEMPT TO INDUCE APOGAMY IN OSMUNDA REGALIS

In the latter part of July, 1912, a large number of prothallia of *Osmunda regalis* were found by the writer in a swamp in the vicinity of Madison. Most of the prothallia at this time were small but had produced numerous antheridia. Some of the prothallia were removed with a depth of about three inches of soil and placed under bell jars in the university greenhouse. Several cultures were kept in a Wardian case where the illumination was very favorable for the normal development of the prothallia. Other prothallia were placed under bell jars and in different parts of the greenhouse where strong light was obtained for the greater part of the year. The latter were watered only from below and great care was exercised to prevent condensation of moisture on the prothallia. In this manner fertilization was prevented for nearly a year and a half. During this period, however, the prothallia grew to a large size, and numerous antheridia and archegonia were produced. Many of the prothallia reached a length of three centimeters. On such prothallia most of the archegonia were formed in acropetal succession, but frequently a number were produced among the older archegonia. In one instance the archegonia on one side of the "midrib" of a prothallium, measuring two centimeters in length, were counted and approximately five hundred were found to be present. Therefore this prothallium had produced about one thousand archegonia.

When the prothallia were freely watered, embryos were pro-

duced in large numbers as a result of fertilization. Hence it is certain that the cultural conditions which were maintained rendered fertilization impossible. The prothallia grown under favorable conditions were smaller, but produced numerous sex organs and embryos only as a result of fertilization.

Since the prothallia for the cultural work were found growing under plants of *Osmunda regalis*, and since no other osmundas were growing in the immediate vicinity, it could hardly be assumed that the prothallia could be referred to any other species. Nevertheless, spores of *O. regalis* were collected and sown in the Wardian case, and in every respect the prothallia grown corresponded to those brought from the field.

The experimental work with *Osmunda regalis* was of especial interest, since Leitgeb (1885) reported in this species the occasional occurrence of apogamy. No one, however, has confirmed the observation. Although Lang (1898), Yamanouchi (1908), Pace (1913), and Nagai (1914) believed that apogamy might be brought about by cultural conditions, Miss Black (1909) and Mottier (1915) were unable to produce a single apogamous embryo by cultural conditions.

SUMMARY

1. The prothallia of a number of species of ferns in which apogamy was discovered were grown under cultural conditions favorable for the development of sex-organs and embryos in non-apogamous species.

2. The prothallia of all the apogamous ferns become heart-shaped before the formation of the embryo. Antheridia are produced on the prothallia of all apogamous forms, but archegonia are formed on the prothallia of only a few forms.

3. The embryo usually appears as a compact region of cells posterior to the apical notch and on the ventral side of the prothallium. In a number of species tracheids are visible among the prothallial cells in the pale portion of the gametophyte.

4. First to make its appearance is the apical cell of the leaf, then that of the root, and later that of the stem. A foot has not, so far, been observed to develop in connection with the apogamous embryos.

5. Either root or leaf or both of these organs may develop on the dorsal side of the prothallium. As a rule, however, they are produced on the ventral side.

6. While the embryo is produced as a rule posterior to the apical notch, it may be formed on a cylindrical or conical "process" and in some instances on the lobes of the prothallium.

7. Several apogamous embryos may be formed on a single prothallium.

8. As in non-apogamous species, secondary prothallia are readily produced, and these form embryos like those of the ordinary prothallia.

9. The "light" area present on the prothallium of some of the apogamous species is rendered more conspicuous in cultures maintained in weak light. The conical or cylindrical "process" increases considerably in length when the prothallia are grown under these conditions. As a result of weak illumination, the embryo is frequently produced as a direct outgrowth of the apical region of the prothallium.

10. By growing the prothallia of *Osmunda regalis* in strong light and preventing fertilization for a year and a half, no embryos were produced apogamously.

11. An investigation extending over a period of six years has resulted in the discovery of apogamy in a large number of ferns. The conclusion that apogamy is of frequent occurrence in the genera *Pellaea*, *Pteris*, and *Aspidium*, is justified on the basis of the many cases so far found in these genera.

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Description of plates 4 and 5

The photomicrographs of the prothallia on PLATE 4, and FIGS. 13, 14, 15, and 18 on PLATE 5, represent a magnification of about twenty diameters. FIGS. 19, 20, and 21 on PLATE 5 show a much higher magnification. The apogamously produced sporophytes were magnified about two and one half times. All the figures were reduced one seventh in reproduction.

PLATE 4

FIG. 1. A ventral view of a prothallium of *Aspidium chrysolobum* just before the beginning of the apogamous embryo.

FIG. 2. A similar view of a prothallium of the same species. The apogamous embryo is represented as a black region posterior to a pale region in the apical portion of the prothallium.

FIG. 3. A ventral view of a prothallium of *Pteris cretica albo-lineata Alexander*. In the apical region a young embryo is developing. In the apical regions established in the lobes tracheids are present.

FIG. 4. A ventral view of a prothallium of *Pteris cretica albo-lineata Alexander*. An embryo with root and leaf has been produced in the new apical region of one of the lobes. On the inner margin of the other lobe a young embryo has also appeared. In the main apical region trachęids are visible.

FIG. 5. A dorsal view of a prothallium of *Aspidium chrysolobum*. The prothallium produced no archegonia. The apogamous embryo appears as a dark region posterior to the apical notch.

FIG. 6. A prothallium of *Pteris cretica albo-lineata*. A tongue-like portion has developed as an outgrowth of the apical region. In the larger secondary prothallium the "pale" region has already appeared.

FIG. 7. A ventral view of a prothallium of *Aspidium hirtipes* with an embryo whose root and leaf are produced on the ventral surface.

FIG. 8. An embryo of *A. hirtipes* with a well-developed root.

FIG. 9. An embryo of *A. hirtipes* with only the leaf well developed.

FIG. 10. An embryo of *A. chrysolobum*, one root of which is on the dorsal surface, and the other on the ventral.

FIG. 11. An embryo of *A. chrysolobum* whose root is on the dorsal surface and leaf on the ventral surface.

FIG. 12. A young sporophyte of *A. hirtipes* with three primary leaves and a single ventral primary root.

PLATE 5

FIG. 13. A ventral view of a prothallium of *Pellaea adiantoides*. The young embryo is surrounded by hairs.

FIG. 14. A prothallium of *Pellaea adiantoides* grown in slightly weaker illumination than that maintained in the Wardian case. The prothallium has become distinctly lobed, and the embryo is developed in the apical region.

FIG. 15. A similar prothallium of the same species. The lobes are still more conspicuous and the embryo has grown to a larger size.

FIG. 16. An embryo of *Aspidium chrysolobum*, one leaf of which is on the dorsal surface and the other on the ventral surface of the prothallium. The long root is also on the ventral surface.

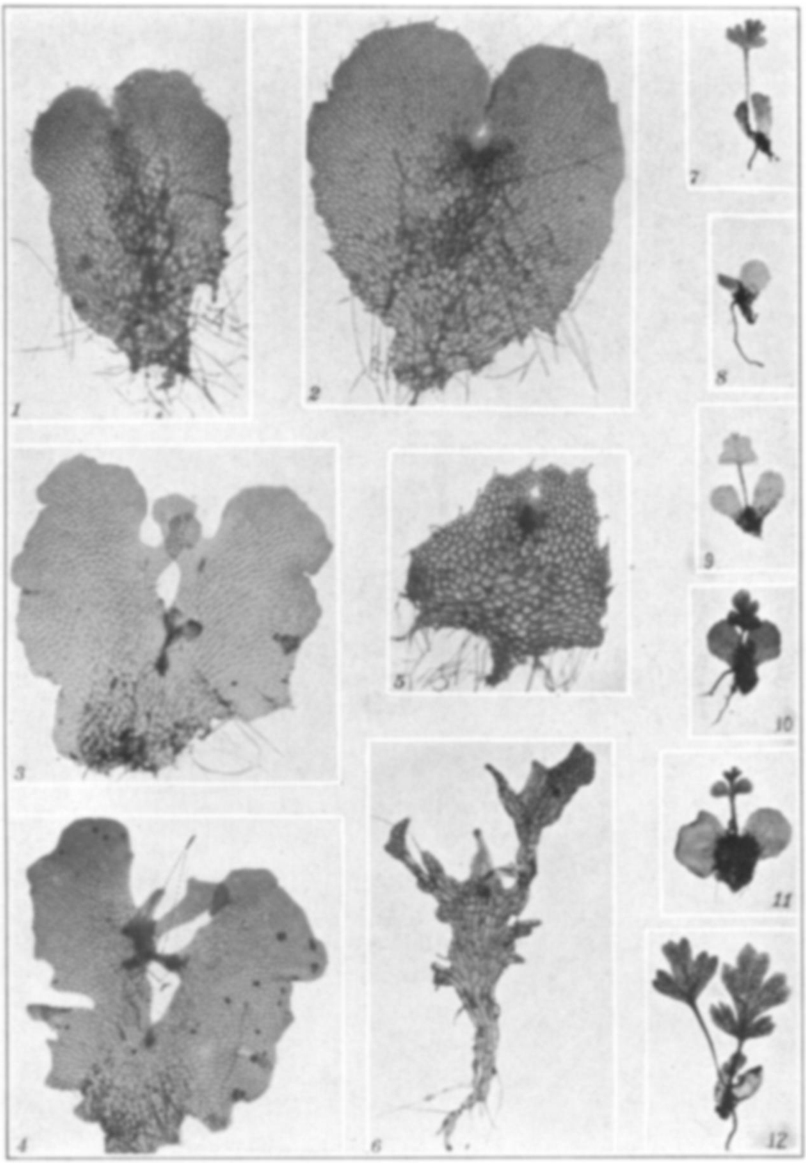
FIG. 17. A portion of a lobed prothallium of *A. hirtipes* bearing two embryos, each of which has a well-developed leaf and root.

FIG. 18. Filaments of a single row of cells of prothallia of *A. hirtipes* grown in weak illumination.

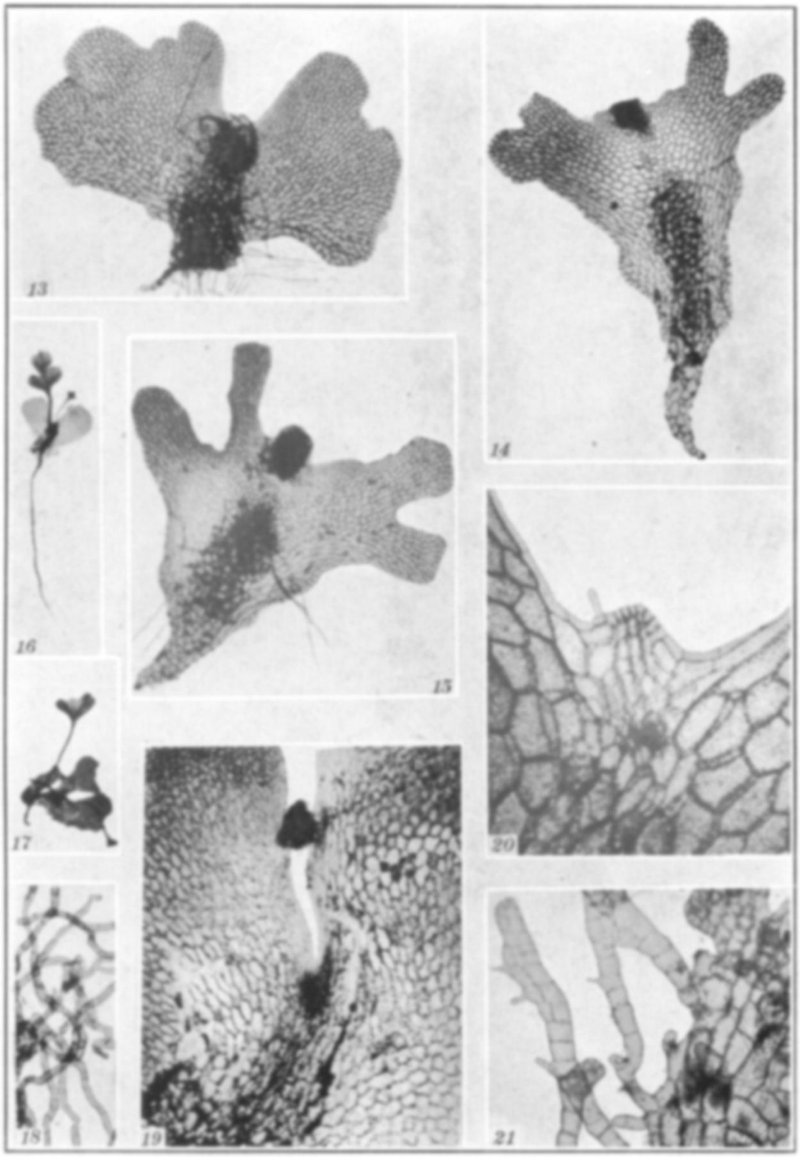
FIG. 19. A prothallium of *Pteris sulcata*, showing the beginning of an embryo in the apical notch. Tracheids pass upward to the young embryo, which has been produced on the inner margin of a lobe.

FIG. 20. An embryo of *A. hirtipes* beginning its development in the apical region. The "pale" region and tracheids are clearly differentiated.

FIG. 21. Secondary prothallia of *A. hirtipes* produced from the margins and surfaces of a prothallium placed in weak light.



STEIL: APOGAMY IN FERNS



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